THE OCCURRENCE OF AN INVERTED HYMENIUM IN *AGARICUS CAMPESTRIS*.

By G. P. Darnell-Smith, D.Sc., F.I.C.

(Plates xci.-xciii.)

In 1917, some mushroom-growers, who were growing mushrooms on a large scale in an old disused railway-tunnel, brought to me, for examination, a number of mushrooms that were unsaleable on account of their appearance. The mushrooms were grown upon large beds of manure, the making of which I had superintended. The manure was fairly moist, it was lightly compacted, and the average temperature was 22°C. Both the stipe and the cap of the specimens were somewhat tough. The cap was quite unusual in appearance. Instead of having the normal, comparatively smooth skin, its surface was broken by one or more black protuberances, 1·25 cm. or more in diameter, that looked like boils (Plate xci., fig.1). It was this appearance that spoilt the sale of the mushrooms. Samples of mushroom-spawn from Sydney, from Adelaide, and from France, were growing in the same tunnel, and providing normal mushrooms; it was only a particular sample of spawn imported from France that was giving rise to these abnormal specimens. A close inspection of the black protuberances showed that they were composed of sinuous, labyrinthiform gill-lamellæ (Pl. lxci., fig.2). They had the appearance of small inverted caps, but no appearance of a stipe could be found. Sections through the cap showed that these structures were quite separate from the normal hymenium, which was present on the undersurface of the cap (Pl. xcii., fig.3).

Sections for microscopical examination were prepared and stained. They showed that the structure of the hymenium on the undersurface of the cap was quite normal.

Sections through the hymenium on the upper surface of the

cap, however, showed it to be quite abnormal in character (Pl. xcii., fig.4). They showed that the "gills" had a most irregular outline, that they varied much in width, and that many of them were hollow. Spores in abundance were produced, both on the external surface of the gills, and on the walls lining the internal cavities. These spores were produced upon enlarged cells, and borne upon sterigmata, as in the case of normal gills. While, however, the normal number of sterigmata is four, cells bearing only one, or only two sterigmata were found, as well as cells bearing the normal number of four (Pl. xciii., figs.5, 6, 7). Crops of mushrooms, showing the abnormal development above described, are not unknown. W. A. Smith, according to Worsdell(1), found, on more than one occasion, crops of mushrooms, every individual of which had an inverted cap on its surface. According to Worsdell, an inverted hymenium may arise (1) through the congenital formation of an inverted cap, or caps, from the earliest stage onwards on the upper surface of the primary cap; (2) through the formation of inverted caps by local invagination of the margin of the primary one. It is held, however, that these two variations really represent the same phenomenon, of which (1) represents the final and completed stage of (2) arising congenitally and isolated.

In my specimens, no trace of the formation of inverted caps by local invagination could be found. Moreover careful examination of mushrooms in the "button"-stage showed, that these irregular gill-lamellæ, on the upper surface of the cap, were in process of formation in the very earliest stages, and long before the velum had separated from the stipe (Pl. xciii., fig.7). There can, therefore, be no question of invagination of the cap in these specimens.

The question arises, what light, if any, does this inversion of the hymenium throw upon the phylogeny of the Agaricaceæ? Is it an expression of a partial reversion to an ancestral character?

That certain spawn has particular characters peculiar to it, is the experience of professional mushroom-growers. In commercial practice, under the influence of the atmosphere and the heat of the manure-beds, the mycelium gets weaker and weaker, and

eventually perishes. "Virgin spawn" obtained from the fields is, therefore, transferred to beds of manure, where it spreads and supplies the grower with a "frank spawn" for growing the edible mushroom. But "often twelve to fifteen kinds of virgin spawn as found in the fields or on heaps of refuse are discarded as useless before a good strain is obtained"(2). That the production of inverted caps was a feature inherent in the spawn under discussion, is shown by the fact that all mushrooms developed from it produced abnormal caps, whereas mushrooms produced from other spawn, under identical conditions, did not.

This phenomenon, together with the characters of the sporophores, lends support to the hypotheses that have been put forward as to the evolution of the cap, and as to the probable origin of the Agaricaceæ, which may be stated briefly as follows:

(*a*). *Evolution of the cap*

1. The production of the horizontally extended, flattened cap-form of fruit from an original, cylindric, dome-shaped form.

2. The relegation of the hymenial tissue to the lower surface of the cap.

3. The formation of "gills" from the original pore or alveolar structure.

(*b*). *Evolution of the* Agaricaceæ.

The most primitive type of fructification is probably that of *Clavaria*, in which a cylindric or club-shaped branch is uniformly covered with hymenium, which extends down the stalk as well for some distance.

"Cases in which the hymenium covers the whole of the upper exposed surface, in the form of a semi-alveolar structure, or labyrinthiform gill-formation, are seen in *Tremella* and *Næmatelia*, and these plants pertain to the Protobasidio-Mycetes; the Tremellineæ have, according to Maire's classification, branched off laterally from the Auriculariaceæ, and it is from these latter that the Agaricaceæ and Polyporaceæ have descended.

In this connection, it is interesting to note that, in one of my specimens that was fairly large, but was obtained in the "button-stage" before rupture of the velum, the whole of the upper surface of the cap is covered with sporogenous tissue (Pl. xciii., fig. 9).

Moreover, this sporogenous tissue is completely covered by a thin membrane, so that there can be no question of its having attained its position through invagination.

The examination of these abnormal mushrooms, therefore, leads to the conclusion, that they represent a partial reversion to an ancestral character. One would hardly expect a complete reversion; and that it is only partial, is demonstrated by the manner in which the spores are borne.

The discharge and disposal of the spores in the Agaricaceæ, according to Buller(4), are brought about, as follows: —

The special conidiophore, or basidium, usually bears four spores, which are discharged successively, and each spore becomes violently detached. The violent discharge of the spores prevents the adhesive spores from massing together, and from sticking fast to the gill-surface. At first, the spore is shot out horizontally; then, under the influence of gravity, it describes a sharp curve, and then falls vertically. The path described by the falling spore has been appropriately called a sporabola. After falling, under the influence of gravity, in the still air between the gill-lamellæ till they reach the exterior, the spores are borne away by the breeze. Basidia, being four sterigmata with four spores attached, were found in my specimens in the inverted hymenium; and it is obvious that, if the spores were discharged in the normal way from the sterigmata and then started to fall under the action of gravity, they would not get free from the hymenium at all, but would fill up the spaces between the gills

We have, therefore, a reversion to an ancestral condition so far as the macroscopic characters are concerned, with a retention of the modern condition so far as the microscopic characters are involved.

LITERATURE CITED.

1. Worsdell, W. C. – Principles of Plant Teratology, Vol. i., p.33 (1915).
2. Aquatias, P.—Intensive culture of Vegetables on the French System, p.153 (1913).
3. Worsdell, W. C.—Principles of Plant Teratology, Vol. i., p.30 (1915).
4. Buller—Researches in Fungi, p.144 (1909).

EXPLANATION OF PLATES XCI.-XCIII.

Plate xci.

Fig. 1.—Abnormal mushroom, showing protuberances of the cap. At the base of the stipe, two small "buttons" are seen.

Fig. 2.—Abnormal mushroom, showing hymenium on the surface of the cap.

Plate xcii.

Fig. 3.—Section of the same.

Fig. 4.—Transverse section through the hymenium on the surface of the cap, showing the irregular character of the gills, and the large spaces in their interior; (× 120).

Plate xciii.

Figs. 5, 6, 7.—Basidia bearing varying numbers of sterigmata (4, 2, 1) from the hymenium in the surface of the cap; (× 480).

Fig. 8.—Section of small "button" much enlarged, showing the formation of lens-shaped areas in the cap containing sporogenous tissue before the separation of the velum.

Fig. 9.—Section of a large "button" (nat. size), showing sporogenous tissue covered with a membrane over the whole upper surface of the cap. The velum has not yet split.